

# CONVERGENT EVOLUTION OF THE 'HOMERIA' FLOWER TYPE IN SIX NEW SPECIES OF *MORAEA* (IRIDACEAE-IRIDEAE) IN SOUTHERN AFRICA<sup>1</sup>

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## ABSTRACT

Six new species of *Moraea*, all with similar small, pale to deep blue-purple flowers and reduced style branches instead of the broad petaloid style branches typical of the genus, are described from the southwest and interior west coast of southern Africa. This flower type, typical of the southern African *Homeria*, was previously known only in a few species of *Moraea*, notably sect. *Polyanthes*, and the flowers of the new species resemble especially those of *M. crispa*. However, of the new species only *M. pseudospicata* appears related to *M. crispa*. The others differ either in vegetative morphology, chromosome number, or in details of the flower, and the unusual flower seems to have evolved independently in at least three of them. *Moraea graniticola*, *M. hexaglottis*, and *M. rigidifolia* are each known from single populations in the southern Namib Desert of Namibia and are referred to sect. *Moraea*. *Moraea worcesterensis*, known from one site near Worcester in the southwest Cape, is probably closely related to *M. algoensis* of sect. *Vieusseuxia*. *Moraea deserticola*, restricted to the Knersvlakte in southern Namaqualand, is allied to *M. speciosa* of sect. *Polyanthes*.

*Moraea* is a widespread African genus of some 115 species of seasonal, corm-bearing perennials of the Old World tribe Irideae of the large and nearly worldwide subfamily Iridoideae. It is the major genus of subtribe Homeriinae, an alliance centered in southern Africa but extending through tropical Africa into the Mediterranean and Middle East. The alliance is characterized by having an astelic corm of a single internode and distinctive, secondarily bifacial leaves (equitant isobilateral leaves are basic in Iridaceae). *Moraea* is the largest of the eight currently recognized genera of the subtribe and occurs almost throughout sub-Saharan Africa, but species are concentrated in highland areas of southeast tropical and southern Africa and in the winter rainfall area of southern Africa. It is relatively well known taxonomically, having been revised recently (Goldblatt, 1973, 1976b, 1977). Despite intensive study, new taxa continue to be discovered, mainly in the winter rainfall areas of South Africa and recently in southern Namibia. Some of these were described in 1982 together with a synopsis of the genus in which 105 species in five subgenera and 12 sections were recognized (Goldblatt, 1982).

Several new species have been discovered since 1982, notably along the arid west coast and interior of southern Africa. The low and variable rainfall of the region is insufficient for species to flower every year, and this combined with the rugged landscape and general inaccessibility leaves this area relatively poorly known botanically. Six new species are described in this paper. *Moraea graniticola*, *M. hexaglottis*, and *M. rigidifolia* are each known from single populations in the southern Namib Desert of Namibia and are referred to sect. *Moraea*. *Moraea worcesterensis*, known from one site near Worcester in the southwest Cape, is probably closely related to *M. algoensis*<sup>2</sup> of sect. *Vieusseuxia*. *Moraea deserticola*, restricted to the Knersvlakte in southern Namaqualand, is allied to *M. speciosa* of sect. *Polyanthes*, while *M. pseudospicata*, from the Nieuwoudtville escarpment, is closely related to the widespread Karoo species, *M. crispa*, also sect. *Polyanthes*.

All six share an unusual feature, a type of flower characteristic of the related genus *Homeria* (Goldblatt, 1980, 1981b) in which the style arms are narrow and inconspicuous and the tepals are similar in color, shape, and disposition. The

<sup>1</sup> Supported by grants DEB 78-10655 and 81-19292 from the United States National Science Foundation. I thank Neil MacGregor, from Glenlyon, Nieuwoudtville, for his hospitality and assistance while in the field; John Lavranos and Inge Pehlemann, who discovered the Namib species and provided living and preserved material; Chris and Bobby van Vuuren, Rosh Pinah Mine, and Rosh Pinah, for their help in the field in southern Namibia; and Dee Snijman, from Compton Herbarium, Kirstenbosch, who rediscovered and drew my attention to the long overlooked *Moraea pseudospicata* and assisted me in recollecting it. I also acknowledge with thanks the drawings of Margo Branch.

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flowers of the new species are similar also in being blue-purple, and, at least in four of them, small and extremely fugacious, opening in the late afternoon and fading at or shortly after dusk. This type of flower was previously known in a few taxonomically isolated species of *Moraea*. Despite their similarities, the flower types probably evolved independently in at least three of them. The adaptive significance of this flower is discussed after an outline of the morphology of the *Moraea* and *Homeria* flower and a review of the new species.

The description of the three new species from Namibia more than doubles the number of *Moraea* species recorded in this country from the two admitted by Sölch (1969), *M. polystachya* and *M. namibensis* (treated as *M. edulis* by Sölch). *Moraea carsonii* has also now been found in the northeast of Namibia bringing the total species of *Moraea* recorded there to six, of which three are endemic. There is in addition at least one and possibly two more known new species of the genus in Namibia, both from the extreme south of the country, at present awaiting description when adequate type material can be assembled.

## MATERIALS AND METHODS

### CYTOLOGY

The chromosomes of five of the six new species were studied. Live material of *Moraea deserticola* was not available. Methods used are the same as those employed in similar studies in Iridaceae (Goldblatt, 1979, 1980). Root tips of sprouting corms were routinely harvested in mid-morning, pre-treated in 0.002 M hydroxyquinoline for seven to eight hours, then fixed in 3:1 absolute ethanol:glacial acetic acid for a few minutes and stored in 70% ethanol. They were hydrolyzed for six minutes in 10% HCl warmed to 60°C, then rinsed in water and squashed in FLP orcein (Jackson, 1975).

### TAXONOMY

Live material of all species except *Moraea deserticola* was examined carefully, and the illustrations were made from living plants. Only cultivated plants of *M. granitica* and *M. hexaglottis* were seen. Herbarium material from important southern African collections was also examined. Measurements were made from live plants except for *M. deserticola*. Delicate parts of the flowers probably shrink some 10–15% and the mea-

surements for *M. deserticola* apply only to dry plants. Flower color fades progressively in dry specimens, eventually changing completely, sometimes becoming darker and usually disappearing. Color notes on collected specimens are desirable and are frequently mentioned by collectors.

Although only two sheets each of *M. granitica*, *M. hexaglottis*, and *M. deserticola* were available, it seems better to describe these species now because they are relatively rare and flower irregularly, so the chance of obtaining more material is small. Also describing these species now is likely to stimulate further plant exploration in the dry interior Namib Desert where *M. granitica* and *M. hexaglottis* occur.

Material examined is cited according to the grid reference system based on geographical degree coordinates of latitude and longitude in current use in southern Africa (Edwards & Leistner, 1971).

### CYTOLOGY

The three Namib Desert species have  $2n = 20$  and a similar karyotype (Fig. 1) with four long acrocentric chromosome pairs, one of which has a small satellite on the distal end of the short arm, and six much smaller submetacentric to metacentric pairs. This matches closely karyotypes found in sect. *Moraea* and is believed to be basic (Goldblatt, 1971, 1976a). *Moraea pseudospicata* and *M. worcesterensis* have  $2n = 12$ .

The karyotype of *Moraea pseudospicata* corresponds well to those of other members of sect. *Polyanthes* in consisting of relatively large acrocentric to submetacentric chromosomes (Fig. 1D, E). Satellites are evident on the distal arms of a long and a short acrocentric chromosome pair. Satellites have been recorded in this position in some populations of *M. crispa* and also on the end of the long arm of a long chromosome pair (Goldblatt, 1980; Fig. 1F) and in *M. polyanthos* of this section. The satellite position in other species of the section such as *M. bipartita* corresponds with that of *M. pseudospicata*.

*Moraea worcesterensis* has a long and a short pair of metacentric chromosomes and a long pair of strongly acrocentric chromosomes with a small satellite at the end of the short arm (Fig. 1F). This karyotype is typical of many species of sect. *Vieusseuxia* (Goldblatt, 1976a, and in prep.), and the karyotype morphology thus accords well with the placement of this species in sect. *Vieusseuxia*.

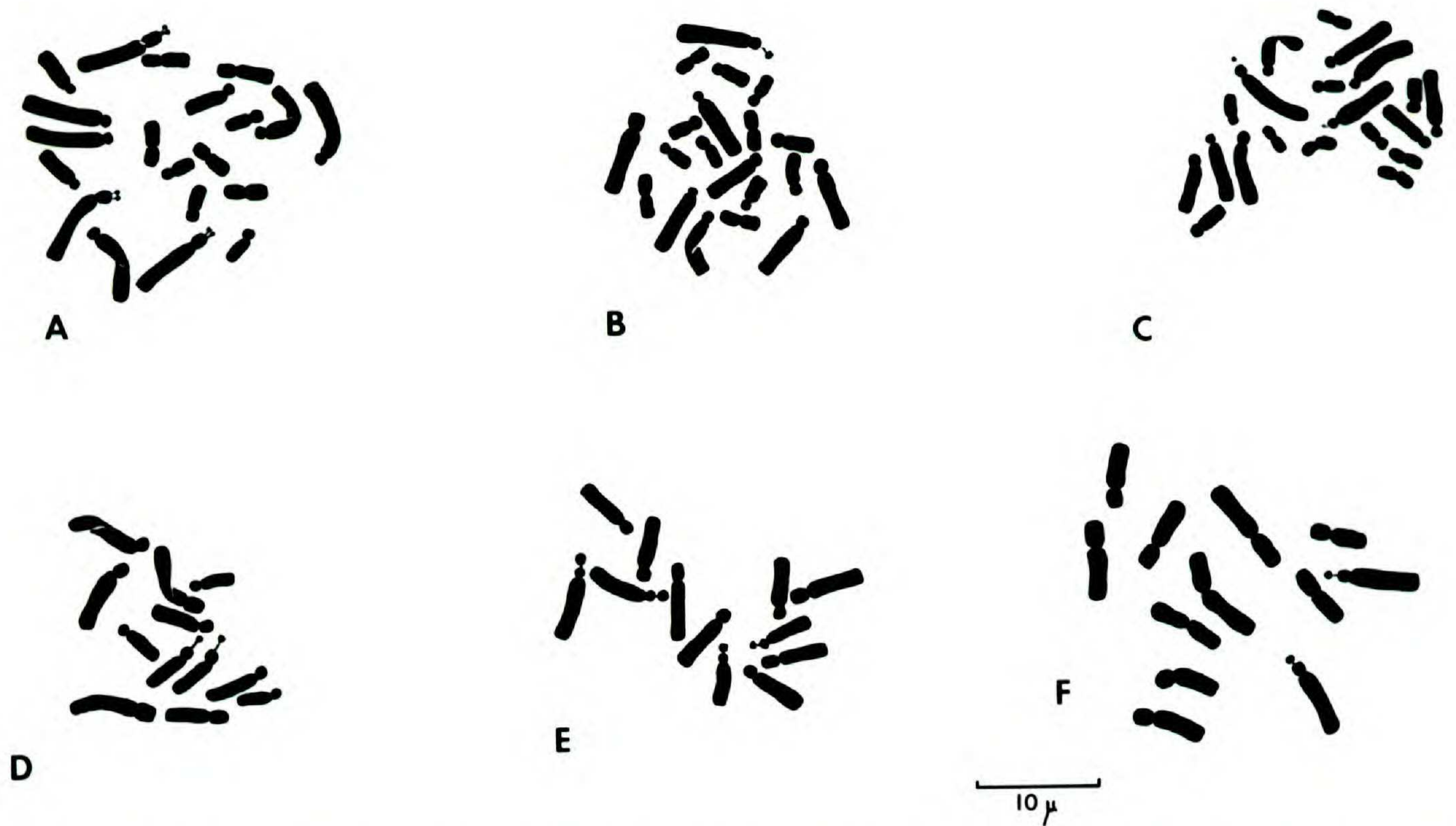


FIGURE 1. Mitotic metaphase figures.—A. *Moraea hexaglottis*.—B. *M. rigidifolia*.—C. *Barnardiella spiralis* for comparison (count but not figure reported in Goldblatt, 1976c).—D. *M. crispa*.—E. *M. pseudospicata*.—F. *M. worcesterensis*. (All to same scale.)

## MORPHOLOGY

### THE BASIC *MORAEA* FLOWER

The typical and apparently basic *Moraea* flower has petal-like, flattened and broad style branches (Fig. 2A) that diverge from the style just above the apex of the filament column. Each style branch has a broad, transverse stigmatic lobe on the upper abaxial surface, and above the stigma it continues as a pair of flat erect appendages, the style crests. These elaborate style branches are like those found in the related *Iris* and *Diets*, the latter believed to be ancestral to both *Moraea* and *Iris* (Goldblatt, 1981a). The *Moraea* flower is *Iris*-like also in having each stamen appressed to the opposed style branch and concealed by the claw of the outer tepal. The outer tepal is somewhat to much larger than the inner and always has a nectar guide at the base of the limb and a well-developed nectary at the base of the claw. The outer and inner tepals may be similarly oriented or the inner may be erect, or somewhat to very reduced, and then trilobed, aristate, ciliate, or completely lacking. In most species of *Moraea* the filaments are united in the lower half into a column around the style, but at least in subg. *Visciramosa* and in *M. ramosis-*

*sima* (subg. *Moraea*) the filaments are contiguous but entirely free.

### THE *HOMERIA* FLOWER

In *Homeria* (31 spp.) the flower is an apparently simple structure (Fig. 2B, D, E). It combines the derived features of united or nearly united filaments and broad tepal claws, which form a cup-like structure including or enclosing all or part of the stamens, as contrasted with apparently unspecialized subequal, similarly disposed inner and outer tepals, and style branches that either lack or have weakly developed paired crests. In addition both whorls of tepals have nectar guides at the base of the limbs and both have nectaries at the base of the claws. In *Homeria* the flower is known to be adapted for fly pollination (Goldblatt, 1981b). Several members of the genus are visited by species of Diptera and not by bees, which pollinate the flowers of most species of *Moraea*. However, some species of *Homeria*, in which the tepal claws are very short and the anthers are held well above the tepals, are secondarily adapted to bee pollination (Goldblatt, 1981b).

Until recently (Goldblatt, 1976a, 1980) all species of *Homeriinae* with the type of flower

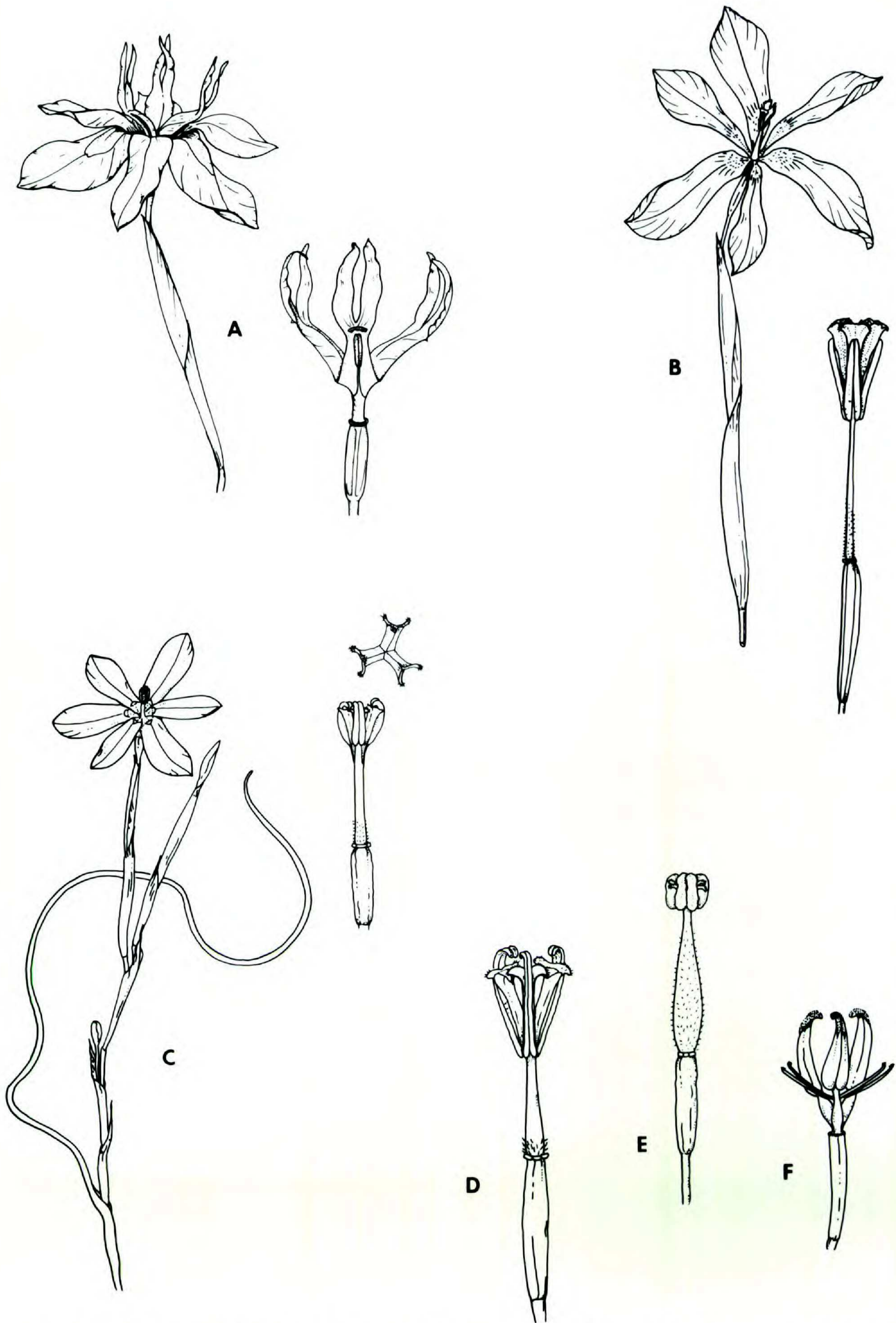


FIGURE 2. Floral features of species of *Moraea* and *Homeria*.—A. *Moraea bipartita*, as typical unspecialized flower typical of *Moraea*, the style branches and stamens drawn separately and enlarged.—B. *Homeria patens*, a typical *Homeria*.—C. *M. crispa*, with a flower modified in a manner similar to *Homeria*, the style branches and stamens much enlarged.—D. Style branches and stamens only of *Homeria elegans*.—E. *H. bifida*.—F. the related genus *Hexaglottis*, especially for comparison with *M. hexaglottis*. Whole flowers life size; separate style branches and stamens,  $\times 2$ .

described above were assigned to *Homeria* despite a lack of uniformity in details of stem, leaf, and corm tunic morphology. Then as a result of a study of chromosome cytology and crossing relationships of the *Homeriinae* (Goldblatt, 1976a, 1980), it became clear that *Homeria* as defined by its characteristic flower alone was artificially constituted and polyphyletic. Information on cytology, interspecific hybridization, and vegetative structure resulted in the transfer of species with  $n = 6$  and karyotypes matching those found in *Moraea* sect. *Polyanthes* to that section; the species with  $n = 10$  were assigned to a new genus *Rheome* that was assumed to be derived from some extinct or at least not yet identified ancestor in *Moraea*.

#### THE NEW SPECIES

The Namib species and *Moraea pseudospicata* resemble the widespread Karoo *M. crispa* (Fig. 2C) in their small, pale to deep blue-purple flowers with short style branches, partly free filaments, and short tepal claws that form a cup including the base of the filament column. The flowers of all these species are extremely fugacious and open after 3 P.M. (even up to 5 P.M.) and fade soon after dark. Only *M. pseudospicata*, with  $n = 6$ , corresponds with *M. crispa* in chromosome number and karyotype, and it seems likely that the two are closely allied. It can be distinguished from *M. crispa* by its sessile lateral inflorescences, large corms with accumulated tunics, and small, globose, irregularly dehiscent capsules.

The three Namib species, all with  $n = 10$ , are regarded as unrelated to *M. crispa* because of the difference in karyotype and are presumed to be allied to species of sect. *Moraea* (or possibly the closely related sect. *Deserticola*), which also have  $x = 10$  and a similar karyotype of four to five long acrocentric pairs and five to six much smaller pairs. *Moraea rigidifolia* has a thick, relatively short and rigid leaf, sessile lateral inflorescences, and fusiform, included ovaries (Fig. 6); *M. graniticola* is acaulescent and has a well-developed perianth tube and a rostrate, fusiform ovary (Fig. 3); and *M. hexaglottis* has short deeply divided style branches, the arms of which extend horizontally below the anthers. The morphological differences between the three Namib species suggest that they are not immediately related to one another. *Moraea rigidifolia* shares its terete leaf and sessile lateral inflorescences with the mono-

typic *Barnardiella* (Goldblatt, 1976c), and it is a possible link between this isolated genus and sect. *Moraea*. The immediate relationships of *M. graniticola* and *M. hexaglottis* are not apparent and their possible relationships and origins are discussed in the systematic treatment.

*Moraea deserticola* resembles the western Karoo *M. speciosa* in its flower and general appearance. Its cytology is not known but it seems certain that it is closely related to *M. speciosa* with which it probably shares a common origin from the widespread southern African *M. polystachya* or its immediate ancestors.

*Moraea worcesterensis* has  $n = 6$  and a karyotype that corresponds well with species of sect. *Vieusseuxia*. It is perhaps most closely related to *M. algoensis* of this alliance, with which it shares a long-lasting, deep blue-purple flower, a slender few-branched stem, and heavily clawed, light brown corm tunics. Its affinity with sect. *Vieusseuxia* has been further established by successful crosses with *M. tripetala*, allied to *M. algoensis*. Control crosses with *M. bipartita* (sect. *Polyanthes*) did not succeed.

Thus, among these six new species of *Moraea*, there appear to be three separate assemblages with a broadly similar *Homeria* type flower. Additional groups with this type of flower are subg. *Visciramosa* (*M. elsiae* Goldbl.), subg. *Vieusseuxia* (including *M. thomsonii* Baker of sect. *Polyanthes*), and some isolated species of sect. *Vieusseuxia* (e.g., *M. lurida* Ker, *M. neopavonia* R. Foster, and *M. insolens* Goldbl.) in which the flower is less obviously *Homeria*-like.

#### ORIGIN AND ADAPTIVE VALUE OF THE FLOWER

There seems little doubt that the *Homeria* flower-type arose several times in the history of the *Moraea*-*Homeria* alliance. It is interesting and probably significant that there does not appear to be a progression of intermediate forms leading to the apparently complex and integrated set of features that comprise the flower. Instead, it seems to have arisen abruptly and it seems likely that one or a very few genic mutations have produced a phenotype so different that the result superficially appears to merit at least species or even generic segregation. The independent origin of similarly structured and colored flowers, even with similar flowering phenology in several species, mostly in the arid interior of western southern Africa suggests that there is some direct adaptive value to this flower. I can only speculate

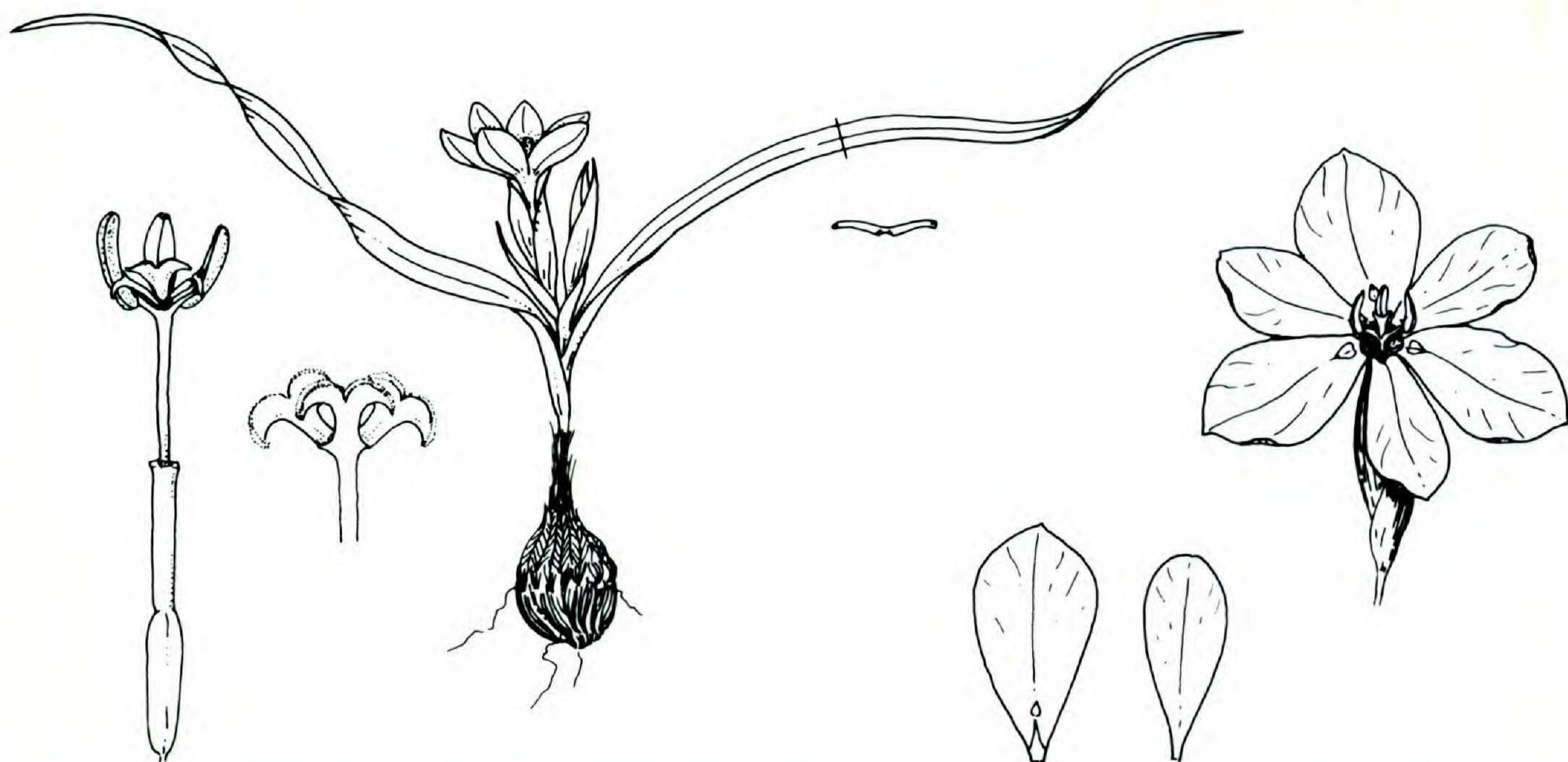


FIGURE 3. Morphology of *Moraea graniticola*. Whole plant,  $\times 0.5$ ; flower, separated tepals, and leaf transverse section, life size; gynoecium and androecium,  $\times 2$ ; separated style branches, much enlarged.

that the color is attractive to small bees, the most likely pollinators. Flowering late in the day may strengthen the chances for pollination at a time when other nectar and pollen sources have been exhausted. Fugaciousness probably protects the flower by limiting its exposure to desiccation and predation from herbivores for the least possible time, still allowing for cross pollination. Like nearly all members of *Homeriinae*, the new species are strongly self-incompatible (the condition in *M. deserticola* is not known).

#### SYSTEMATIC TREATMENT

##### SECTION *MORAEA*

1. *Moraea graniticola* Goldbl., sp. nov. TYPE: Namibia. Aus (26.16): southern Namib Desert, Aus townlands, in sand around granite domes, ca. 1,300 m (cult. Kirstenbosch Botanic Gardens in 1983) (CB), *Lavranos & Pehlemann 20007* (holotype, WIND; isotype, MO). FIGURE 3.

Plantae parvae plus minusve acaulescentes, foliis duobus secundo parvo vel vestigiale, caule ramis prope terram fasciculatis, floribus caeruleis, tubo ca. 5–6 mm longo, tepalis 16–20 mm longis, unguibus partem inferiorem columnae filamentorum includentibus, limbis horizontalibus extensis, filamentis 5–6 mm longis in columna connatis supra ad 1 mm liberis et divergentibus, antheris ad 3.5 mm longis divergentibus, ovario fusiforme rostrato 7–8 mm longo, ramis styli ad 2 mm longis bifurcatis quam antheris brevioribus.

Plants, low, acaulescent or nearly so, to 5 cm

high. *Corm* 2.5–3.5 mm diam., with dark brown, coarsely fibrous tunics, live corm to 8 mm diam. *Leaves* usually 2, the second small and vestigial, grey-green, channeled, spreading, white in the midline, somewhat twisted, margins undulate, to 20 cm long and 6 mm wide. *Stem* subterranean or produced just above the ground, usually with 1–3 branches clustered near the base. *Inflorescence* *spathes* herbaceous, 2.5–3 cm long, the inner somewhat membranous and slightly shorter. *Flower* with a perianth tube, blue-violet with yellow nectar guides, tepal claws ascending and enclosing the lower part of the filament column, limbs spreading horizontally; *perianth tube* 5–6 mm long, white; *outer tepals* 18–20 mm long, obovate, 9–11 mm wide, claws to 3 mm long, the inner to 17 mm long and 9 mm wide. *Filaments* 5–6 mm long, united in a white cylindrical column, free and diverging in the upper 1 mm; *anthers* to 3.5 mm long, diverging, cream. *Ovary* 7–8 mm long, fusiform, included in the *spathes*, with a short sterile beak to 2 mm long; *style* dividing near the base of the anthers, branches diverging, 2 mm long, deeply bilobed, the lobes diverging, to 1 mm long, stigmatic towards apices. *Capsule* unknown. *Chromosome number*  $2n = 20$  (*Lavranos & Pehlemann 20007*).

*Flowering time.* September to early October (in cultivation).

*Distribution.* Southern Namib Desert, in sand around granite domes, known only from around Aus. Figure 5.

*Relationships.* The flower of *Moraea granitica* resembles closely those of *M. crispa*, *M. pseudospicata*, and *M. rigidifolia*, but as outlined in the introduction, the vegetative morphology and chromosome cytology indicate that the resemblance is due to convergence. It seems most likely that *M. granitica* is most closely related to sect. *Moraea* in which all species except *M. rigidifolia* and *M. hexaglottis* have a typical *Moraea* flower with well-developed style branches and crests. However, it differs from all members of this section in having the perianth and filaments united below into a short tube. The tube is completely closed and apparently functions to raise the flower above the spathes for better display to pollinators. The acaulescent habit is unknown elsewhere in the section and is rare in *Moraea*, being restricted to the four species of sect. *Acaules*. This is an apparently monophyletic alliance distinguished by contractile pedicels that raise the tubeless flowers above the spathes and later draw them back for the completion of fruit development. It seems unlikely on morphological grounds that *M. granitica* is related directly to *M. rigidifolia* despite the similarity of their subequal, short-clawed spreading tepals and short, narrow crestless style branches.

*History.* *Moraea granitica* was discovered in 1982 by John Lavranos and Inge Pehlemann in a sterile state, in dry ground around granite boulders on the townlands at Aus, in southern Namibia. The town lies inland from Luderitz on the rail line to the interior, and towards the inner edge of the Namib Desert. Corms given to Kirstenbosch Botanic Gardens flowered in 1983 when the specimens that comprise the type collection were prepared. *Moraea granitica* is apparently rare in the wild, even at the single site from which it is known. It is likely that the species occurs elsewhere in rocky parts of the southern Namib where there is normally some winter precipitation.

**2. *Moraea hexaglottis* Goldbl., sp. nov.** TYPE: Namibia. Witpütz (27.16): southern Namib, farm Aub, Huib Plateau, ca. 80 km N of Rosh Pinah, 1,200–1,400 m (BB), *Lavranos & Pehlemann 21704* (holotype, MO; isotype, WIND). FIGURE 4.

Plantae parvae, 8–10 cm altae, folio solitario gracili, caule ramoso, floribus caeruleis, tepalis ca. 10 mm longis, unguibus partem inferiorem columnae filamentorum includentibus, limbis horizontalibus extensis, filamentis 3 mm longis in columna connatis supra ad 1

mm liberis et divergentibus, antheris ad 2.5 mm longis divergentibus, ovario cylindrico anguste, ca. 3 mm longo, ramis styli bifurcatis a basi, ramulibus ad 2 mm longis, inter apices filamentorum extensibus.

Plants small, 8–10 cm high. *Corm* 10–15 mm diam., with coarse brown fibrous tunics. *Leaf* solitary, basal, slender, and apparently terete but linear and channeled, with tightly inrolled margins, sometimes somewhat twisted above, about twice as long as the plant. *Stem* somewhat flexuose, 1–2-branched, stem bracts subtending the branches 12–18 mm long, herbaceous, becoming dry above, axes flexed slightly below the spathes. *Inflorescence spathes* green, becoming dry and pale straw colored above, 16–19 mm long, the outer about half to nearly as long as the inner. *Flowers* blue-violet with pale yellow nectar guides on outer tepals; *outer tepals* 12–14 mm long, claw vestigial, limb spreading almost from the base, 6–7 mm wide, obovate; *inner* smaller than the outer, 10–12 mm long, lanceolate. *Filaments* ca. 4 mm long, united in the lower half in a smooth cylindrical column, diverging above; *anthers* 3–4 mm long, ascending, yellow. Ovary narrow, cylindrical, ca. 3 mm long, at least partly exerted from the spathes; *style* dividing at the apex of the filament column, branches divided almost to the base into paired slender tapering arms extending upwards between the filaments, the arms 2.5–3 mm long, apically stigmatic, crests lacking. *Capsules* globose, 4–6 mm diam.; *seeds* angular. *Chromosome number*  $2n = 20$  (*Lavranos & Pehlemann 21704*).

*Flowering time.* September to October, flowers opening in mid-afternoon, at about 4 P.M., fading in early evening.

*Distribution.* Known from only one site on the Huib Plateau at about 1,300 m, in southern Namibia in silt on black limestone. Figure 5.

*Relationships.* The small, blue-violet flowers with spreading, subequal tepals of *Moraea hexaglottis* are very like those of *M. rigidifolia* and the Karoo species *M. crispa*. However, the short style branches, each divided almost to the base into a pair of slender, ascending arms are unlike those of any other species of *Moraea* and resemble those of the related genus *Hexaglottis* (5 spp.). In *Hexaglottis* the filaments are united only towards the base and the style arms are more slender than in *M. hexaglottis*, and the flowers are always yellow. In addition, *Hexaglottis* has  $x = 6$  (Goldblatt, 1971, and in prep.) in contrast to  $n = 10$  in *M. hexaglottis*. It is clear that *M.*

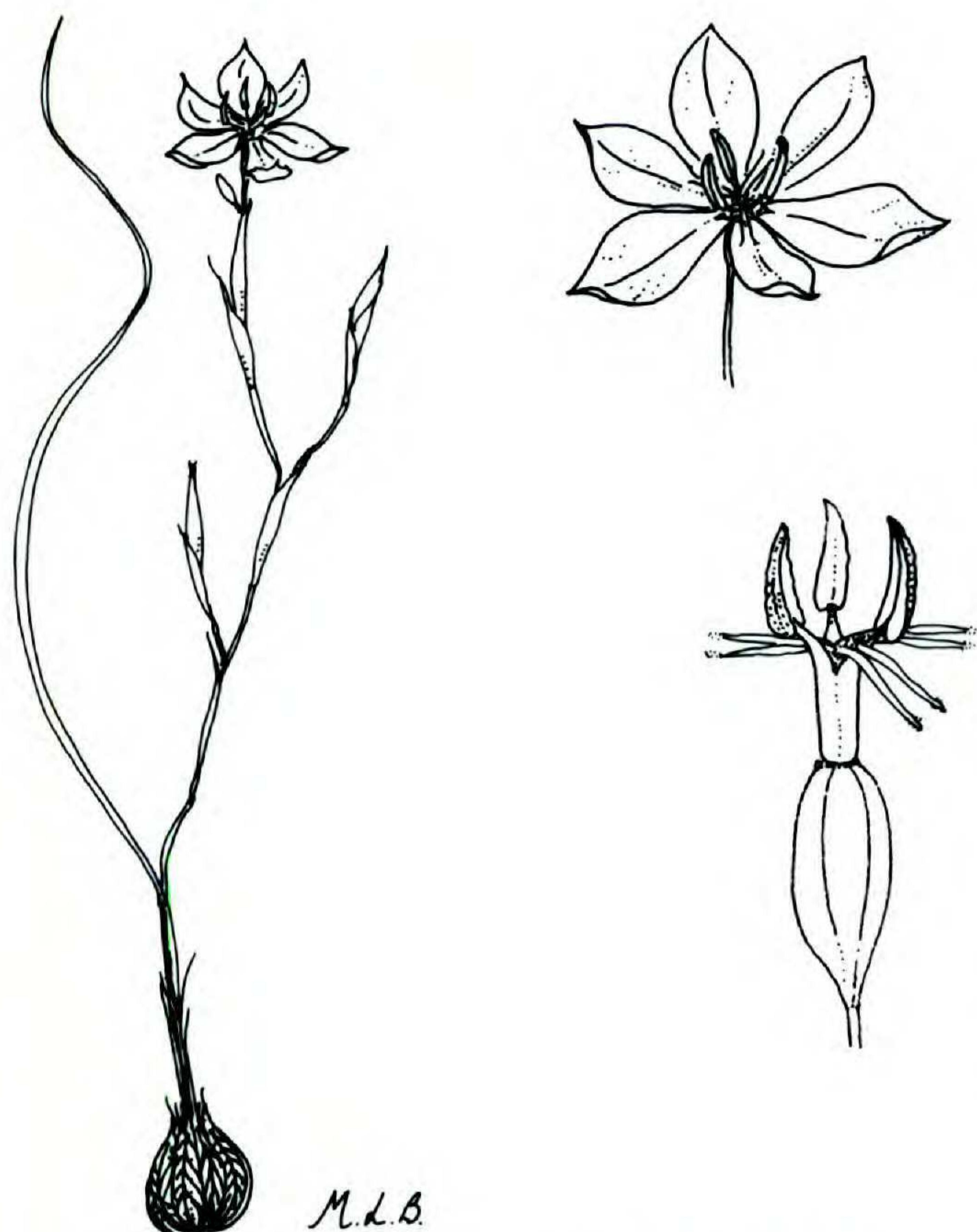


FIGURE 4. Morphology of *Moraea hexaglottis*. Whole plant,  $\times 0.5$ ; flower, life size; gynoecium and androecium,  $\times 2$ .

*hexaglottis* and *Hexaglottis* acquired similar style branches independently, but the similarity is striking. *Moraea hexaglottis* is probably most closely related to *M. tortilis* of sect. *Moraea* based on overall similarity in vegetative morphology.

**History.** The species was discovered by John Lavranos and Inge Pehlemann in 1983 on the Huib Plateau in southern Namibia. It is known from a few sites on the farm Aub and is, according to Lavranos, widespread there. It probably occurs elsewhere on the western part of the Huib Plateau that receives limited precipitation in the winter. The habitat is described as silt on black limestone, quite different from the rocky granite where the other two southern Namibian species grow. The specific epithet refers to the six slender style arms or tongues that are characteristic for the species.

3. *Moraea rigidifolia* Goldbl., sp. nov. TYPE: Namibia. Witpütz (27.16): southern Namib Desert, rocky granite flats ca. 40 km N of Rosh Pinah, farm Süd Witpütz, ca. 1,100 m (DA), Goldblatt 7016 (holotype, WIND; isotypes, MO, NBG, PRE, S, US, WAG). FIGURE 6.

Plantae 7–12 cm altae, folio solitario fistuloso falcato ad recurvo, caule inflorescentibus lateralibus sessilibus, raro infra ramoso, floribus caeruleo-malvinis, tepalis 13–18 mm longis, unguibus partem inferiorem columnae filamentorum includentibus, limbis horizontalibus extensis, filamentis 4–5.5 mm longis, in columna connatis supra ad 1.3–2 mm liberis et divergentibus, antheris 2.2–3 mm longis divergentibus, ovario lineari-fusiforme rostrato 5–7 mm longo, ramis styli 2–2.5 mm longis bifurcatis quam antheris brevioribus.

Plants slender, 7–12 cm high. *Corm* 2–3 cm diam., with dark brown, coarsely fibrous tunics accumulating to form a thick layer and extending upwards in a neck, live corm ca. 8 mm diam. *Leaf* solitary, basal, terete, to 3 mm diam., fistulose, pithy inside, falcate to recurved. *Stem* simple or branched from below, bearing several sessile inflorescences above, stem bracts dry, brown, to 2.5 cm long. *Inflorescences* sessile except the terminal, *spathes* herbaceous, becoming dry and brown above at anthesis, 1.7–2.2 cm long, the outer slightly shorter than the inner. *Flowers* blue-mauve with cream nectar guides on the outer tepals, the claws forming a shallow cup round the base of the filament column, limbs spreading horizontally; *tepals* lanceolate, 14–18 mm long, claw 3–4 mm, limb 6–7 mm wide, widest in the upper third, the inner 13–15 mm long, 5–6 mm wide. *Filaments* 4–5.5 mm long, united below, free in the upper 1.3–2 mm and diverging, forming a slender smooth cylindrical column; *anthers* 2.2–3 mm long, diverging, white. Ovary linear-fusiform, included in the spathes, 5–7 mm long, with a sterile beak 1–2 mm long; *style* dividing at the apex of the filament column, branches diverging, 2–2.5 mm long, bilobed above and stigmatic apically, reaching to mid anther level, crests lacking. Capsules not known. *Chromosome number*  $2n = 20$  (Goldblatt 7016).

**Flowering time.** Late September to October, flowers opening in late afternoon, at about 4:30 P.M. and fading in early evening at about 7 P.M.

**Distribution.** Rocky granite flats, in the southern Namib Desert north of Rosh Pinah. Figure 5.

**Relationships.** The small, pale blue-mauve flowers of *Moraea rigidifolia* have subequal tepals with short claws that enclose the lower part of the filaments and divergent anthers appressed to short narrow style branches. They closely resemble those of the Karoo species *M. crispa*. My initial presumption was that the two were closely related. However, *M. rigidifolia* has a base num-



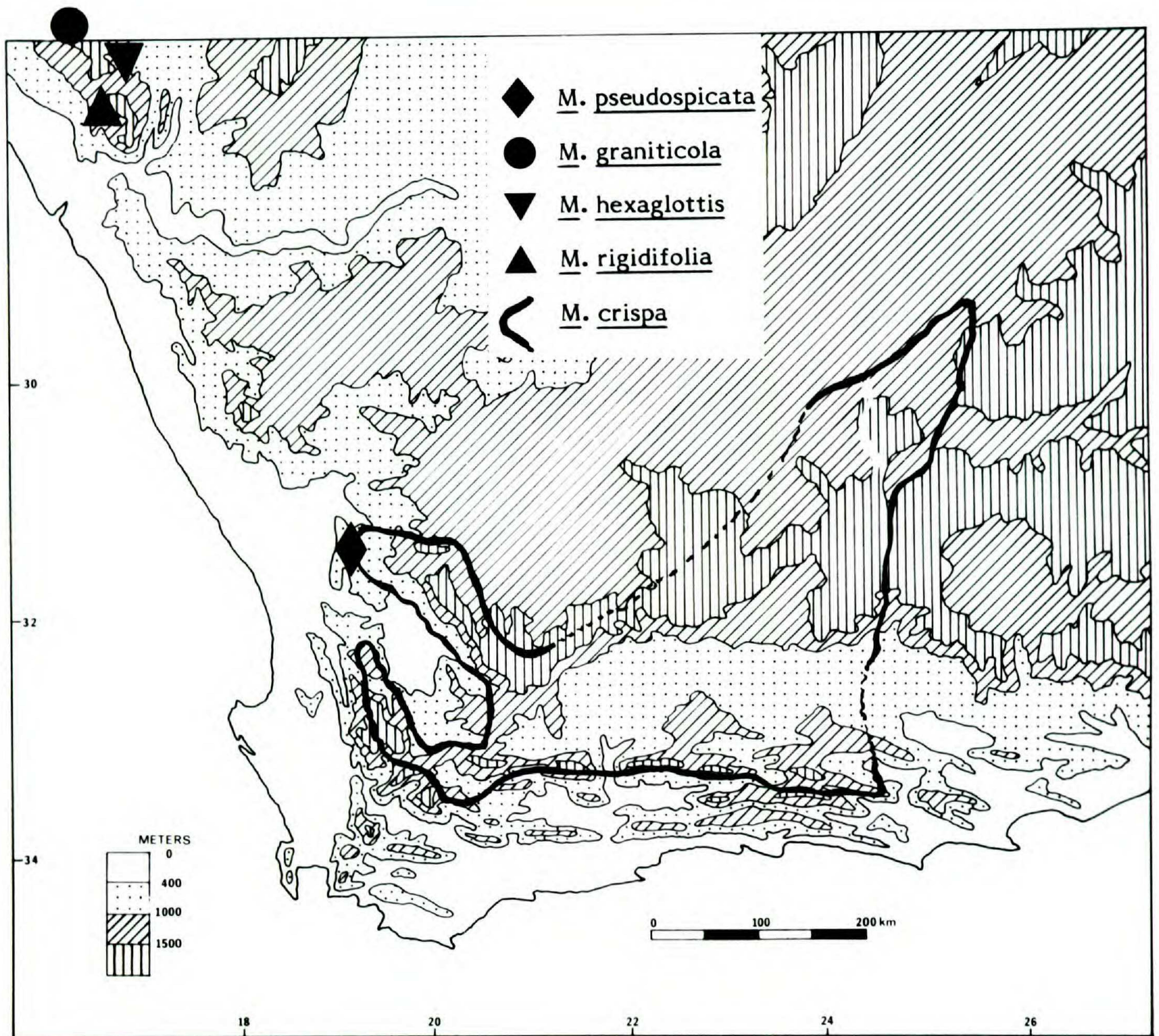


FIGURE 5. Geographical distribution of *Moraea pseudospicata*, *M. graniticola*, *M. hexaglottis*, *M. rigidifolia*, with the range of *Moraea crispa* heavily outlined for comparison.

ber of  $x = 10$  and karyotype quite different from that of *M. crispa* and of sect. *Polyanthes* generally. The basic chromosome number for *Moraea* is  $x = 10$  and both number and the details of the karyotype of *M. rigidifolia* conform with species of subg. *Moraea* as well as with the monotypic Namaqualand *Barnardiella*. The cytological evidence is regarded here as a more reliable indicator of relationship, and *M. rigidifolia* is presumed to be allied to species of sect. *Moraea* or sect. *Deserticola*. In its general habit *M. rigidifolia* resembles quite closely *Barnardiella spiralis*, which has similar, though more often smaller corms, a single terete but slender leaf, and sessile lateral inflorescences with relatively short and subequal spathes. *Barnardiella* differs in having a long slender tube composed of sterile

ovary tissue (Goldblatt, 1976c) and a subsessile ovary located in the base of the spathes. Details of the style and anthers of *Barnardiella* differ only slightly from those of *M. rigidifolia* and it seems likely that *M. rigidifolia* is close to the line that gave rise to *Barnardiella*. The slender ovary of *M. rigidifolia*, which is sterile in the upper 1–1.5 mm, is perhaps a link with the unusual ovary found in *Barnardiella*.

*Moraea rigidifolia* is easily recognized by its very unusual thick and relatively short terete leaf. The swollen leaf, which consists of green tissue surrounding a firm white pith-like parenchyma, is so striking that *M. rigidifolia* can immediately be identified from this feature alone.

*Distribution.* *Moraea rigidifolia* is known only from a single locality in southern Namibia, on

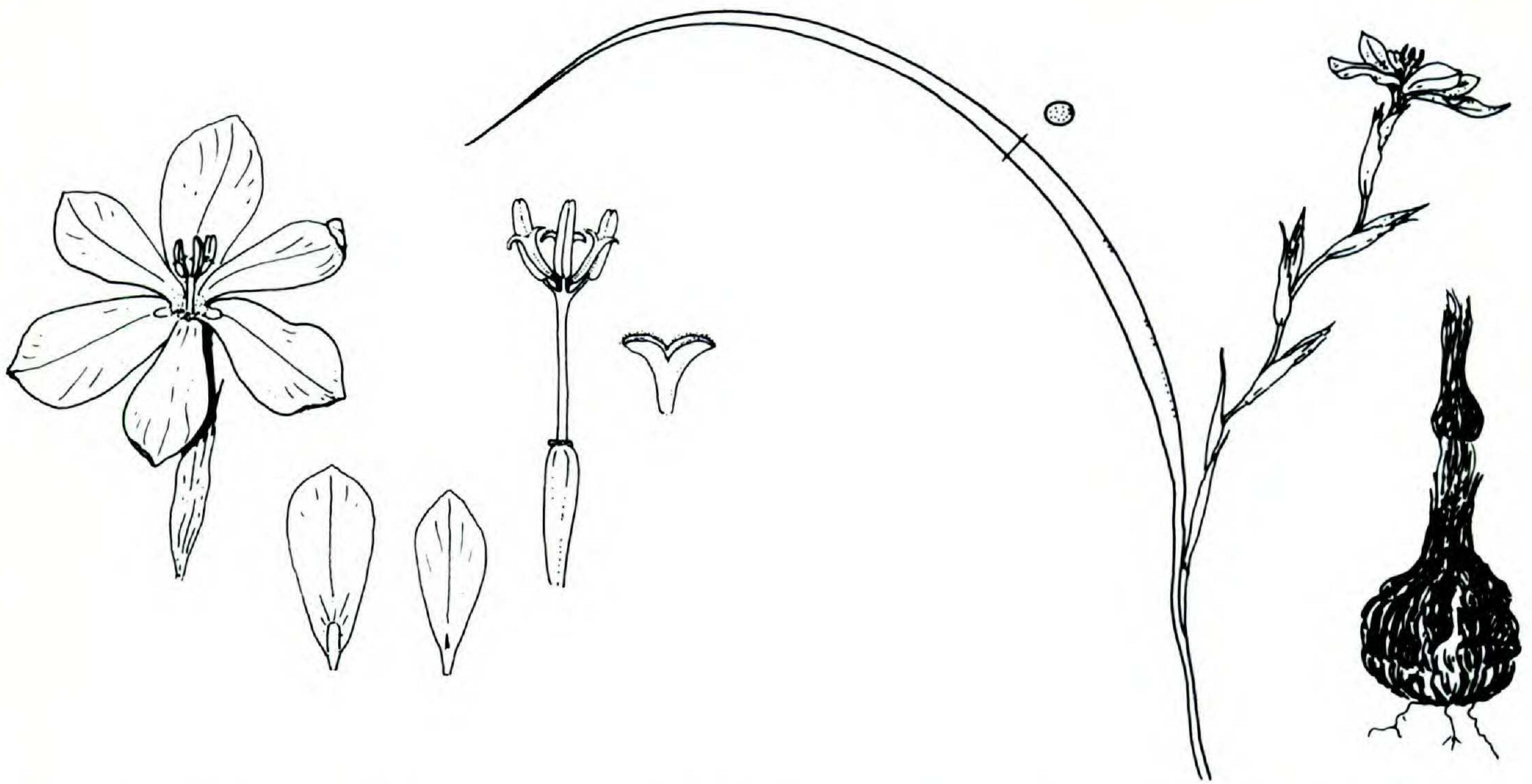


FIGURE 6. Morphology of *Moraea rigidifolia*. Whole plant, corm, and leaf transection,  $\times 0.5$ ; flower and separated tepals, life size; gynoecium and androecium,  $\times 2$ ; separated style branch, much enlarged.

the farm Süd Witpütz, some 35 km north of the mining settlement of Rosh Pinah near the Orange River. It was discovered by John Lavranos and Inge Pehlemann in 1982. In the very good spring season of 1983 I revisited the locality and collected ample flowering specimens. The habitat of *M. rigidifolia* is rocky and consists of thin soil and low outcrops of weathered granite. It is locally fairly common in open places, the corms often wedged in cracks in rock, but only shallowly buried. *Moraea rigidifolia* probably occurs elsewhere in the rocky southern Namib Desert, which is poorly known botanically. Owing to its inconspicuous and fugacious flowers that open only in the late afternoon and early evening, it is easily overlooked.

*Additional material examined.* NAMIBIA. Southern Namib Desert. 29.16 (Witpütz) rocky granite flats ca. 40 km N of Rosh Pinah, farm Süd Witpütz, ca. 1,100 m (DA), Lavranos & Pehlemann 19104 (MO).

#### SECTION POLYANTHES

4. *Moraea pseudospicata* Goldbl., sp. nov. TYPE: South Africa, Calvinia (31.19): Cape Province, Glenlyon, E of Nieuwoudtville, dry Dwyka tillite flats (AC), Snijman 783 (holotype, NBG; isotypes, K, MO, PRE, S, STE, WAG). FIGURE 7.

Plantae 15–40 cm altae, folio solitario gracili canaliculato in latere adaxiali, caule interdum infra ramoso, inflorescentibus lateralibus sessilibus, floribus

caeruleo-malvinis, tepalis 11–16 mm longis, unguibus partem inferiorem columnae filamentorum includentibus, limbis horizontalibus extensis, filamentis 4–6.5 mm longis, in columna connatis vel supra liberis et contiguis, antheris 2–4.5 mm longis contiguis, ovario globoso ca. 2 mm diam., ramis styli 1–1.5 mm longis antheris occultis.

Plants slender, 15–40 cm high. *Corm* 3–5 cm diam., with tough, blackish fibrous tunics usually accumulating to form a thick layer and extending upwards in a neck, live corm ca. 1 cm diam. *Leaf* solitary, basal, slender, apparently terete but narrowly grooved on adaxial surface and margins tightly inrolled, straight or weakly twisted. *Stem* simple or 1–2-branched from below, bearing several sessile inflorescences at the upper nodes, stem bracts dry, brown, to 2.5 cm long, distinctly darker on the veins. *Inflorescences* sessile except the terminal, *spathes* subequal, partly concealed by the subtending bracts, dry and straw-colored at anthesis, also darker on the veins, 2–2.5 cm long. *Flowers* blue-mauve with deep yellow nectar guides on inner and outer tepals, the claws forming a shallow cup round the base of the filament column, limbs spreading horizontally; *tepals* lanceolate, 11–17 mm long, claw ca. 2 mm, limb 3.5–4 mm wide, widest in the upper third, the inner tepals ca. 1 mm shorter than the outer. *Filaments* 4–6.5 mm long, united entirely or free in the upper two-thirds but contiguous, forming a slender, smooth cylindrical column; *anthers* 2–4.5 mm long, erect and contiguous, yellow. *Ovary*



FIGURE 7. Morphology of *Moraea pseudospicata*. Whole plant and corm,  $\times 0.5$ ; flower and separated inflorescence with fruit, life size.

globose, ca. 2 mm long; *style* dividing at about mid anther level, branches narrow, ascending, 1–1.5 mm long, stigmatic apically, initially concealed by the anthers, reaching to the upper third or slightly exceeding the apex of the anthers; crests lacking. *Capsules* globose, 2–4 mm diam., membranous and semitransparent, not loculicidal but fragmenting irregularly; seeds several, dark brown, ca. 1 mm long. *Chromosome number*  $2n = 12$  (Goldblatt 6543).

*Flowering time.* December to March, flowers opening after 3:30 P.M. and fading in the early evening.

*Distribution.* Rocky clay flats, in karroid scrub, in the Nieuwoudtville district from the hills north of the town extending south to Lokenberg and possibly to the dry interior valleys of the Cedarberg. Figure 5.

*Relationships and variation.* *Moraea pseudospicata* resembles the widespread Karoo species *M. crispa* in both flower structure and general aspect. The pale blue-mauve flowers are almost identical in their subequal tepals with short erect claws that form a short, narrow tube, which includes the lower part of the filament column. The filaments and anthers are slightly shorter in *M. pseudospicata*, and the anthers are nearly erect and so conceal the narrow and short style branches. In *M. crispa* the anther and style branches diverge strongly, and although the style branches are shorter than the anthers, they can easily be seen. The two species also have the same chromosome number,  $n = 6$ , and karyotypes with acrocentric to submetacentric chromosomes that characterize sect. *Polyanthes*, and it seems certain that the two are closely allied. *Moraea pseudospicata* differs mainly in its sessile lateral inflorescences and in the dry chaffy stem bracts and spathes. Its capsules also differ from those of *M. crispa* in being slightly smaller, in having almost membranous walls, and in apparently dehiscing irregularly rather than along the locule sutures as in nearly all other species of *Moraea*. *Moraea pseudospicata* is also distinctive in its flowering time, mid to late summer, in an area of complete summer drought, and at the time of flowering the leaf is usually dry and often broken. In the summer dry western Karoo and adjacent Cedarberg where both *M. pseudospicata* and *M. crispa* occur, *M. crispa* blooms from October to November and rarely into December.

The relatively few collections of *Moraea pseudospicata* indicate little variability except for the filaments, which may be almost entirely united or free but contiguous in the upper half. This feature does not appear to be correlated with geographical distribution.

An unusual collection, Galpin 11170 (K, PRE), from Nieuwoudtville, has a strong resemblance to *Moraea pseudospicata*. It has small but apparently deep blue-purple flowers and the characteristic sessile lateral inflorescences of *M. pseudospicata*, but the capsules, of which there are several in nearly mature state, are elongate and fusiform, about 10 mm long, and have a well-developed beak about 1 mm long. This is quite different from the globose capsule of *M. pseu-*

*dospicata*. Examination of the poorly preserved and few flowers reveals that the filaments are 3.5 mm long, and at least free above (indistinct below), the anthers are contiguous and very short, about 1.2 mm long, and the ovary is about 4.5 mm long. Other details are not visible. It seems likely that the collection represents a species closely allied to *M. pseudospicata*, distinguished at least by a different capsule (that contains apparently larger seeds), smaller anthers, and darker colored flowers. The flowering time noted on the single collection is November, another difference with *M. pseudospicata*, which has not been recorded in flower earlier than December, and usually flowers later.

*History.* The first known collections of *Moraea pseudospicata* were made by Carl Zeyher, who in 1829 journeyed to Namaqualand (Gunn & Codd, 1981) and the mouth of the Orange River 'Reise nach Kamiesberg, Boschmanland, bis zur mundung des Garip.' Several duplicates, distributed as *Ecklon & Zeyher Irid. 32* are in herbaria that have good sets of Ecklon and Zeyher duplicates. Only the sheet at Stockholm has complete locality data 'Onderboksveld, Bluht December, 4 hohe.' From this it seems almost certain that their gathering was made near present-day Nieuwoudtville, this general area still being sometimes called the Lower Bokkeveld. Other early records of this species include plants from the 'Cedarberg,' collected by Thode and from Lokenberg, south of Nieuwoudtville, collected by Acocks. All these collections lay unidentified or placed with either *Hexaglottis* or *M. crispa*. In 1980 Dierdre Snijman of the Compton Herbarium at Kirstenbosch showed me a collection of a species she had made near Nieuwoudtville that included well-pressed flowers. The specimens struck me as unusual both in morphology and in their flowering time. In 1982 I relocated the species at two sites to the north of Nieuwoudtville and made extensive collections. Once this species had been identified as a new and distinctive *Moraea*, I was able to assign to it the earlier records cited above. Specimens were found at a third site closer to Nieuwoudtville in 1984, and this collection has been selected as the type material.

*Additional specimens examined.* SOUTH AFRICA. CAPE: 31.19 (Calvinia) near Nieuwoudtville, Charlies Hoek, between Loeriesfontein Road and Klipkoppies (AC), *Snijman 98* (NBG), *Goldblatt 6542* (MO); rocky clay flats on the road to Rondekop, E of Nieuwoudtville, *Goldblatt 6543* (MO, NBG, PRE, S); Glenlyon, E of Nieuwoudtville, dry Dwyka tillite flats (AC), *Snij-*

*man 783* (K, MO, NBG, PRE, S, STE, WAG); Lokenburg (CA), *Acocks 17555* (PRE).

WITHOUT PRECISE LOCALITY: "Reise nach Kamiesberg, Boschmanland, bis zur Mundung des Garip," *Zeyher as Ecklon & Zeyher Irid. 32* (73.12) (LD, MO, P, S 'Bluht December 4 hoh Onderboksveld'); Cedarberg, *Thode A2076* (PRE).

**5. *Moraea deserticola* Goldbl., sp. nov.** TYPE: South Africa. Vanrhynsdorp (31.18): Cape Province, Knersvlakte, farm Quaggas Kop, Zout River (BC), *Hall 5089* (holotype, NBG; isotype, MO).

Plantae 35–45 cm altae, cormo ca. 1 cm diam., foliis 2–3 linearibus canaliculatis, floribus albis pallide caeruleis in reverso, unguibus cupulatis columnam filamentorum includentibus, tepalis 30–36 mm longis, filamentis 8–10 mm longis connatis in columna cylindrica, antheris 5–6.5 mm longis erectis contiguis, ovario plus minusve obovato, 6–7 mm longo, rubro venoso, ramis styli brevibus horizontaliter extensis supra antheras.

Plants 35–45 cm high. *Corm* ca. 1 cm diam., with tunics of dark brown to blackish fibers. *Leaves* 2–3, linear and channeled, 2–3 mm wide, about as long as the stems, margins becoming tightly inrolled when dry, the lower basal, upper cauline. *Stem* simple or 1–3-branched from the upper nodes, the branches subtended by sheathing bract leaves 2.5–4 cm long. *Spathes* 3.3–4 cm long, herbaceous, the outer about two-thirds as long as the inner. *Flowers* pale blue or white with pale blue on the reverse of the tepals and fading pale blue, with yellow nectar guides at the base of the limb of the inner and outer tepals, tepal claws ascending and forming a wide cup including the filament column, limbs extended horizontally; *tepals* 30–36 mm long, claw ca. 12 mm long, limb 18–20 mm long and 10–11 mm wide, the inner slightly smaller than the outer. *Filaments* 8–10 mm long, united into a smooth slender cylindrical column; *anthers* 5–6.5 mm long, erect, contiguous, appressed to and initially concealing the style. Ovary 6–7 mm long, narrowly obconic, exerted from the spathes, with conspicuous reddish veins; *style* dividing into 3 short horizontal lobed branches just above the apex of the anthers; branches ca. 1 mm long, crests lacking. *Capsule* more or less obovoid, 9–10 mm long, red-veined, seeds many, angled. *Chromosome number* unknown.

*Flowering time.* June to August.

*Distribution.* Stony slopes and flats in the Knersvlakte between Vanrhynsdorp and Nuwerus. Figure 8.

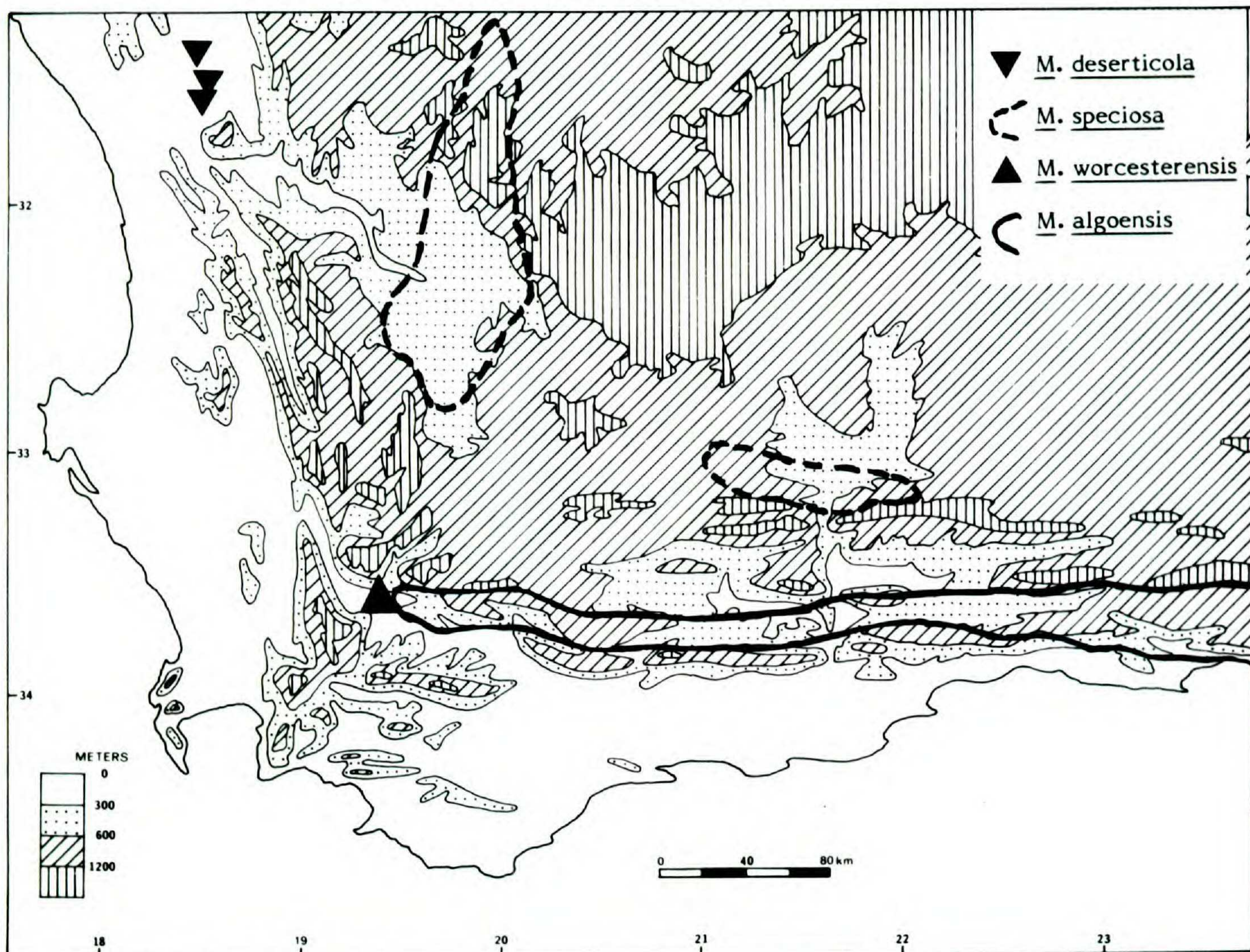


FIGURE 8. Geographical distribution of *Moraea deserticola*, with the range of the closely allied *M. speciosa* indicated by the broken line, and *M. worcesterensis*, with the range of the putatively related *M. algoensis* indicated by the heavy, unbroken line.

**Relationships.** The large and deeply cupped flower of *Moraea deserticola* with its nearly equal tepals and long conspicuous anthers is strongly reminiscent of *M. speciosa*, a species of the drier parts of the western Karoo. It seems certain that the two species are closely allied although they differ greatly in vegetative morphology. The long style surrounded by the contiguous anthers, and short, broadly-lobed style branches held above the anthers when the stigmas are receptive are exactly the same in both species. Except for a slightly smaller size, the flowers and all floral parts of *Moraea deserticola* are apparently identical to those of *M. speciosa*. The leaves of *M. deserticola* are narrow and few, and only the lowermost is basal while the other two or three are spaced well apart along the stem. Moreover, the leaves are straight and narrowly channeled and the stem bears only a few branches towards the apex. In contrast, *M. speciosa* has a thick fleshy well-branched stem and several relatively short

and broad basal leaves that are often undulate or twisted. *Moraea deserticola* can also be distinguished by its strongly dark purple-veined ovary, a feature not evident in *M. speciosa*.

**History and distribution.** The species was first discovered in 1967 by P. A. B. van Breda, in the Knersvlakte, the arid low rolling country in southern Namaqualand that is so extraordinarily rich in low-growing succulents. Due to the limited material available and inadequate preservation, the collection could not at first be identified although it did not seem to be any known species. It was recollected in 1981 by Harry Hall and two years later by Jan Vlok but has not been seen since. The collection made by Hall is barely sufficient for a type but it seems preferable to describe the plant now rather than wait indefinitely hoping to find more specimens. Perhaps also now that the species is named others will be encouraged to search further for it.

The species is probably rare in the wild, but

as it has been found at three sites in the Knersvlakte, it probably occurs widely in the area. Most likely the plants are scattered and inconspicuous, and added to this, they probably flower only when good rains have fallen in this arid area.

*Additional specimens examined.* SOUTH AFRICA. CAPE: 31.18 (Vanhynsdorp) 9 km NW of Vanhynsdorp near the gypsum mines, sandy soil, *Vlok 655* (MO); Varsrivier, ca. 11 mi. N of Vanhynsdorp, *van Breda 4018* (PRE).

SECTION *VIEUSSEUXIA*

6. *Moraea worcesterensis* Goldbl., sp. nov. TYPE: South Africa. Worcester (33.19): Cape Province, stony sandstone flats at Worcester West (CB), *Goldblatt & Snijman 6977A* (holotype, NBG; isotypes, K, MO, PRE, S, STE, US). FIGURE 9.

Plantae 12–25 cm altae, tunicis fibrosis unguiculatis, folio solitario canaliculato, floribus atropurpureis tepalis inaequalibus expansis, exterioribus 15–17 mm longis, interioribus 13–15 mm longis, unguibus ca. 3 mm longis, filamentis liberis supra, antheris 4 mm longis, ramis styli angustis apicibus bilobis.

Plants 12–25 cm high. *Corm* globose, 15–20 mm diam., tunics brown, fibrous, often heavily clawed, sometimes accumulating to form a thick covering. *Leaf* solitary, basal, linear, canaliculate, somewhat to about twice as long as the stem. *Stem* simple or with a single branch, erect or flexed at the upper nodes. *Spathes* herbaceous, dry and dark brown above, 28–35 mm long, the outer about half as long as the inner. *Flowers* dark violet-purple with yellow nectar guides on all tepals; *outer tepals* 15–17 mm long, claw ascending, ca. 3 mm long, limb laxly extended horizontally, 12–14 mm long and ca. 9 mm wide; *inner tepals* similarly oriented, smaller, 13–15 mm long and 4–5 mm wide. *Filaments* 5–6 mm long, united below, free in the upper 2 mm; *anthers* 4 mm long, exceeding the style branches, yellow. Ovary ca. 5 mm long, nearly cylindrical but narrowing below, *style branches* narrow, less than 1 mm wide, diverging and appressed to the opposed anther, becoming bilobed apically and stigmatic at the ends of the lobes, *crests* lacking. *Capsules* narrowly obovoid, to 10 mm long. *Chromosome number*  $2n = 12$  (*Goldblatt 6977A*).

*Flowering time.* September.

*Distribution.* Known only from stony flats west of Worcester, in mixed fynbos and renosterfeld. Figure 8.

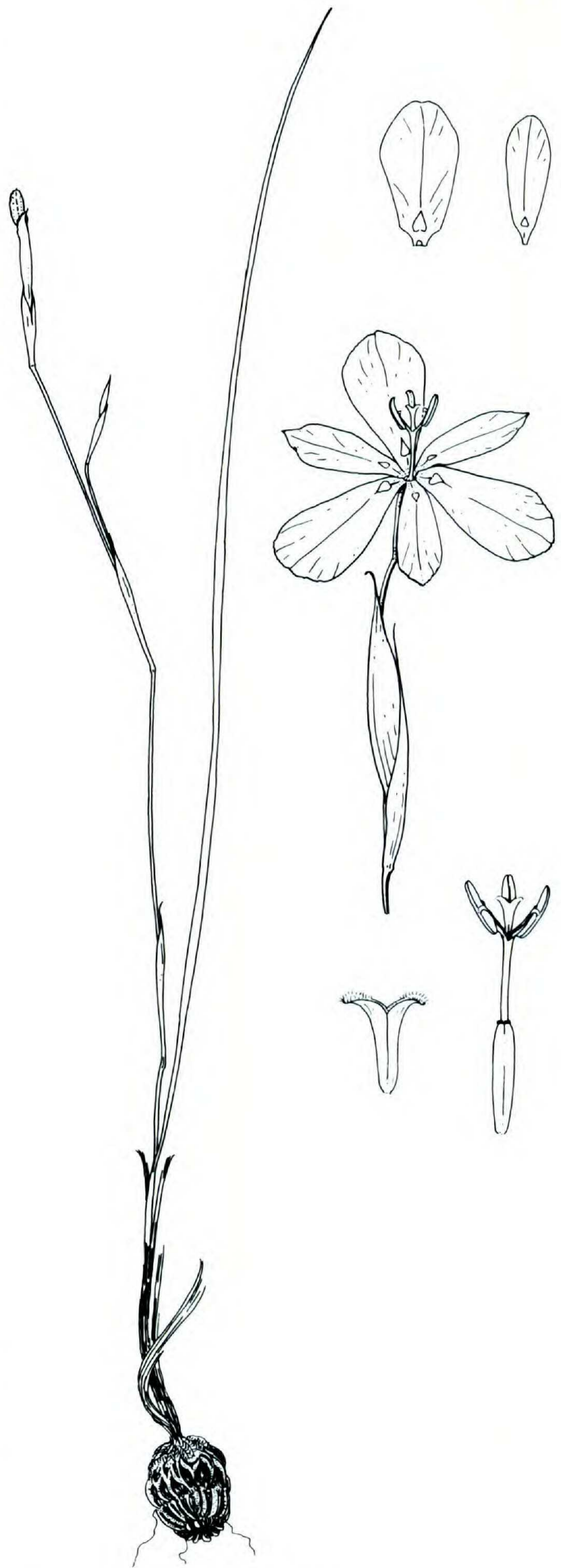


FIGURE 9. Morphology of *Moraea worcesterensis*. Whole plant,  $\times 0.5$ ; flower and separated tepals, life size; gynoecium and androecium,  $\times 2$ ; separated style branch, much enlarged.

*Relationships.* *Moraea worcesterensis* is probably closely related to the widespread southern Cape species *M. algoensis*, despite its very different flowers. It has more or less spreading tepals, both whorls of which have nectar guides, a slender filament column, and very reduced, narrow style branches, shorter than the subtending anthers and lacking crests. *Moraea algoensis* has a typical *Moraea* flower with large inner tepals, the claws of which touch the broad petaloid style branches to conceal the anther and stigma lobe. In *Moraea algoensis* the inner tepals are relatively broad for sect. *Vieusseuxia*, most species of which have narrow, linear, trifid to ciliate inner tepals. The general flower color of *M. worcesterensis* and *M. algoensis* is the same, and the corms conform to the type found in many species of the section. The single and basal leaf and reduced number of branches are also consistent with placement in this section.

The general similarity of *Moraea worcesterensis* to *M. polyanthos* in sect. *Polyanthes* is probably due to convergence for the *Homeria* type of flower. Thus although the flowers of the two species are similar, the vegetative structure is very different. *Moraea polyanthos* has (two to) three to five leaves, several branches, and blackish corm tunics of a tough wiry texture, all characteristics that seem to be significant in determining the relationships of species of *Moraea*.

*History.* *Moraea worcesterensis* was apparently first discovered in the spring of 1983, by me, Dierdre Snijman, and Jane Turnbull, both of the National Botanic Gardens, in Worcester West, a rapidly developing suburb of Worcester. It is now extinct at the type locality but probably occurs elsewhere along the foot of the Langeberg Mountains.

#### LITERATURE CITED

- EDWARDS, D. & O. H. LEISTNER. 1971. A degree reference system for citing biological records in southern Africa. Mitt. Bot. Staatssamml. München 10: 501–509.
- GOLDBLATT, P. 1971. Cytological and morphological studies in the southern African Iridaceae. J. S. African Bot. 37: 317–460.
- . 1973. Contributions to the knowledge of *Moraea* (Iridaceae) in the summer rainfall region of South Africa. Ann. Missouri Bot. Gard. 60: 204–259.
- . 1976a. Evolution, cytology and subgeneric classification in *Moraea* (Iridaceae). Ann. Missouri Bot. Gard. 63: 1–23.
- . 1976b [1977]. The genus *Moraea* in the winter rainfall area of Southern Africa. Ann. Missouri Bot. Gard. 63: 657–786.
- . 1976c [1977]. *Barnardiella*: a new genus of the Iridaceae and its relationship to *Gynandriris* and *Moraea*. Ann. Missouri Bot. Gard. 63: 309–313.
- . 1977 [1978]. Systematics of *Moraea* (Iridaceae) in tropical Africa. Ann. Missouri Bot. Gard. 64: 243–295.
- . 1979. Chromosome cytology and karyotype change in *Galaxia* (Iridaceae). Pl. Syst. Evol. 133: 161–169.
- . 1980. Redefinition of *Homeria* and *Moraea* (Iridaceae) in the light of biosystematic data, with *Rheome* gen. nov. Bot. Not. 133: 85–95.
- . 1981a. Systematics, phylogeny and evolution of *Dietes* (Iridaceae). Ann. Missouri Bot. Gard. 68: 132–153.
- . 1981b [1982]. Systematics and biology of *Homeria* (Iridaceae). Ann. Missouri Bot. Gard. 68: 413–503.
- . 1982 [1983]. A synopsis of *Moraea* (Iridaceae) with new taxa, transfers and notes. Ann. Missouri Bot. Gard. 69: 351–369.
- GUNN, M. & L. E. CODD. 1981. Botanical Exploration of Southern Africa. A. A. Balkema, Cape Town.
- JACKSON, R. C. 1975. Chromosomal evolution in *Haplopappus gracilis*: a centric transposition race. Evolution 27: 243–256.
- SÖLCH, A. 1969. Iridaceae. In H. Merxmüller (editor), Prodröm einer Flora von Südwestafrika 155: 1–12.